Chapter

CAPACITY LIMITS IN VISUAL SHORT-TERM MEMORY

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ABSTRACT

Visual short-term memory (VSTM) is the system that temporarily holds relevant visual information that is useful for a particular ongoing cognitive task. Most studies on VSTM have particularly focused on its storage capacity. Even though they have not yet resolved the fundamental question of why there is a capacity limit in the first place, those studies have converged to the conclusion that VSTM is extremely limited in capacity, holding only about three to four objects simultaneously. In this chapter, I will review the different techniques that have been used to reveal the capacity limits in VSTM as well as the different factors that have been shown to influence this capacity. This review will consider both behavioural and Neuroimaging work.

1. INTRODUCTION

Imagine Bob, a healthy young man, watching a movie scene in which an actor is sitting in a car next to his new date. The actor is dressed with a jeans and a red check shirt. The camera then moves to a close-up of the actor's face, full of admiration for his new guest, and finally comes back to the initial shot. His shirt is now a blue check shirt. Bob would notice this evident and unforgivable editing error if he can spot the mismatch between this new information and the old one that must be retrieved from memory since not visible anymore. In other words, Bob needs to have a cognitive system that allows him to encode and store visual information and to make use of it when that information is no longer in view. This system is called *visual short-term memory* (VSTM) (or *visual working memory*).

The very existence of a short-term memory dedicated to the maintenance of recently perceived visual information has only been established at the end of the 60's and in the early 70's. Before that, studies about the storage of visual information were conducted within the context of iconic memory, a very short-lived memory (i.e., less than half a second) and regarded as the persistence of the initial perceptual image (Neisser, 1967; Sperling, 1960). For the visual information to be maintained for longer time than half a second, researchers then thought that the information had to be verbally recoded (Sperling, 1963; 1967). This idea can probably be accredited to the experimental paradigms adopted during that period, which particularly encouraged verbal coding of visual information. For example, in the colour memory study of Brener (1940), coloured slides were serially presented to participants, who then had to verbally report the colour names in the order they were shown. The results revealed that about seven colours could be accurately reported, which coincides, rather predictably given the nature of the recall procedure, to the prototypical verbal memory span of seven items (Miller, 1956). Even in the famous study of Sperling (1960), in which participants were instructed to report all the stimuli that were briefly presented, verbal short-term memory could have play a major role. Not only by the nature of the stimuli that were used (i.e., letters and digits) but also by the task itself that entailed to write down the characters that were reported, requiring therefore a translation of the visually presented information into a verbal code.

The works of Posner in the 60's and Phillips in the 70's have been extremely influential for the acknowledgement of a specific system than can store the visual aspect of information, and that for longer time than the simple persistence of the sensory experience. For instance, Posner and colleagues (Posner & Keele, 1967; Posner, Boies, Eichelman, & Taylor, 1969) conducted a simple letter matching task in which two letters were sequentially presented to participants. The letters were displayed in either upper (e.g., "A") or lower case (e.g., "a"). The task was to decide whether the two letters were the same or different, irrespective of the physical presentation. The results revealed faster response times when the letters had the same appearance as compared to when they visually differed. Those findings suggest, perhaps indirectly, that the visual representation of a stimulus can be stored in memory, and therefore that a VSTM system exists.

A more direct demonstration of the existence of a post-iconic visual memory was provided by Phillips (1974) using a procedure that, for the first time, assessed VSTM performance without being contaminated by verbal short-term memory. Phillips used the change detection paradigm in which two arrays of complex visual stimuli (i.e., partially-filled grids of dots), which were completely unfamiliar and pretty hard to verbally encode, were successively presented to participants and separated by a brief retention interval. The two grids of dots were either similar or different by having one cell more or less filled. The task was to detect a change between the two grids. Various retention interval durations and different levels of complexity, defined by the number of cells, were used. The results revealed that at short retention intervals (<250 ms), change detection performance was high and unaffected by the complexity of the grids. However, at longer intervals, performance declined as a function of the number of cells in the arrays. Those findings clearly demonstrate the distinction between a high-capacity, but short-lived, iconic memory representation and a limited-capacity, but longer-lasting, VSTM representation.

What characterises VSTM the most is probably its extremely limited capacity of storage. As we will see throughout this chapter, research has consistently shown that only a few pieces of information can be simultaneously held in VSTM. This high limitation is commonly exemplified in the literature by the phenomenon known as 'change blindness'. Change blindness refers to the remarkable failure of individuals to notice significant changes in visual scenes when these changes occur across brief perceptual interruptions such as blank intervals, blinks, eye movements, etc. (see

the review by Simons & Rensink, 2005). For example, in an experiment conducted in natural, real-world social situation, Simons and Levin (1998) observed that 50% of people in the test did not notice that the man in front of them has turned into a different person after a very brief visual interruption. In view of this, researchers would not be surprised if Bob, our romantic movie fan from the example given at the start of this chapter, actually fails to detect the colour change of the actor's shirt[1]. To detect a change, the initial information has to be first encoded and maintained in memory, and then retrieved to enable the comparison process with the new input. Change blindness can be explained by a breakdown of any of those memory stages (i.e., encoding, storage, retrieval) but basically suggests that our VSTM is quite poor at representing properly a large amount of visual information.

In this chapter, I will first review the different methods and procedures that have been employed to measure the storage capacity of VSTM (section 2). Then, I will provide a synthesis of the different factors that have been found to modulate this capacity (section 3).

2. MEASURING THE CAPACITY OF VISUAL SHORT-TERM MEMORY

2.1. Behavioural measures

The capacity of VSTM refers to the maximum of visual items that can be held, and is usually estimated by the number of items that can be correctly recognised or recalled after their presentation (Logie, 1995). Most studies on VSTM capacity have indeed used either a recognition paradigm or report procedure. To some extent, these two methods are similar as they both involve the presentation of a sample array, which consists of one or more visual items that must be remembered, followed by a short retention interval, and finally by a memory test. In addition, in both paradigms, memory performance declines as the number of items in the sample array (i.e., the set size) increases.

In the recognition paradigm, the memory test involves a comparison between a second array (i.e., test array) that follows the retention interval, and the initial sample array. The task typically requires a simple same/different judgement. The test array may consist of either a single-probe or a whole-display. In a single-probe test, only one item is presented at test and the task is to decide whether that particular item comes from the sample array. In a whole-display test (also known as the change detection paradigm – Phillips, 1974), all the items presented within the sample array are shown again at test, except that on some trials one of those items is different. The task requires detecting that change. The observer's ability to match the information between the two sequentially presented arrays, or to detect a mismatch, accounts for his memory capacity. In other words, the assumption behind the failure to recognise a previously presented object, or to detect a change, is that the object was not properly encoded, stored, or retrieved from memory.

Although Phillips (1974) was the first to use the recognition paradigm to assess VSTM performance, it cannot be assured that Phillips' results actually provide a pure estimate of VSTM capacity of storage. In Phillips' study, grids of dots were used as stimuli and the simultaneous presentation of the dots may have led participants to encode a configuration of the dots as a gestalt

[1] Movie editing mistakes are far from being a rarity. For example, according to MovieMistakes.com, 394 editing errors have been found in the movie "Apocalypse Now" (i.e., one error every 25 seconds!), 298 errors in "Harry Potter and the Prisoner of Azkaban", 271 errors in "Star Wars", etc. What is even more extraordinary is the fact that very few viewers, even the most devoted fans, have ever detected a single one of those mistakes.

figure rather than a set of distinctive items (e.g., two dots form a line, three dots form a line or a triangle, etc.). As the whole configuration (i.e., the gestalt figure) made by the dots often changes with the addition or removal of one dot, the task could have been based purely on configuration change detection. Importantly, recent research has shown that the encoding of a configuration, as well as the detection of a configuration change, do not necessarily require encoding and maintaining each item individually (Delvenne, Braithwaite, Riddoch, & Humphreys, 2002; Delvenne & Bruyer, 2006; Jiang, Olson & Chun, 2000).

The first convincing and systematic measure of VSTM capacity in a recognition paradigm was provided by Luck and Vogel (1997) (see also Vogel, Woodman, & Luck, 2001, for a full report). Rather than using indistinct items (like the dots in Phillips' study), Luck and Vogel (1997) used simple distinct features, such as different colours and orientated lines (Figure 1). While participants in Phillips's study could have relied on the dots configuration to make their change detection judgments, those from Luck and Vogel's study undeniably had to discriminate between the items and to memorise each of them independently. The authors observed that change detection performance remained almost flawless when there were 4 or less items in the sample array, but declined dramatically and rather consistently with larger numbers of items. This abrupt decrease in memory performance when more than four items are presented led the authors to suggest that the capacity of VSTM is about 3-4 items. The recognition paradigm, as a tool for measuring VSTM capacity, has since been used in many studies (e.g., Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007; Delvenne & Bruyer, 2004, 2006; Delvenne, Cleeremans, & Laloyaux, 2010; Jiang et al., 2000; Wheeler & Treisman, 2002; Xu, 2002a, amongst many others). Those studies, among which some have used quantitative estimates of capacity using the Pashler/Cowan K equation (Cowan, 2001; Pashler, 1988), have all reached the same conclusion, namely that VSTM is severely limited in storage capacity.

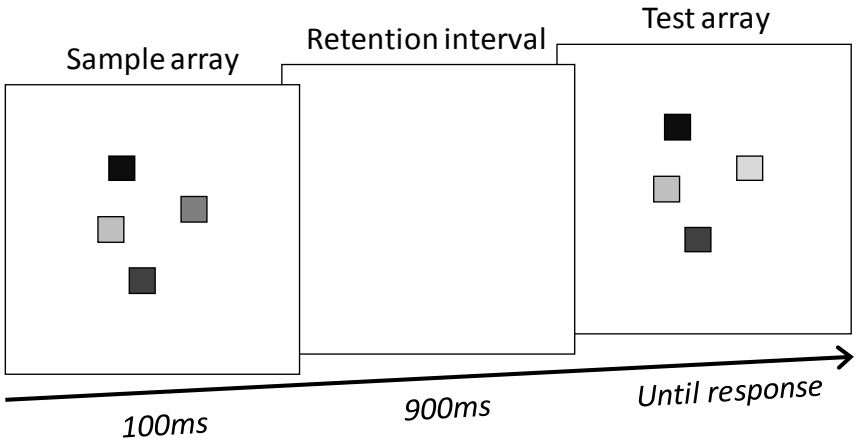


Figure 1. Example of a colour change detection task. The task is to decide whether the colours in the test array are the same as, or different from those in the sample array. Different grey levels represent different colours.

Although the recognition paradigm is a simple procedure that can be used to test the ability to remember an item with sufficient fidelity to discriminate it from a different object, it provides little information about how well the item is remembered. In order to provide a continuous measure of the fidelity of the memory representations, a second class of VSTM studies has recently emerged in which a report procedure is used (Bays, Wu, & Husain, 2011; Umemoto, Drew, Ester, & Awh, 2010; Wilken & Ma, 2004; Zhang & Luck, 2008). For example, Wilken and Ma (2004) have developed a paradigm in which participants were briefly presented with a number of coloured items and then,

after a short retention interval, were cued to report the exact colour of one of the items by adjusting a continuous colour wheel (Figure 2). The authors found that the precision of reports declined systematically as the number of items increased, suggesting that as more items are held in memory, the precision of the stored information decreases. Using the same procedure, Zhang and Luck (2008) found that although the rate of random guessing was low from 1 to 3 items, the amount of detail maintained about the items decreased, suggesting that VSTM holds 1 item with greater fidelity than 3 items.

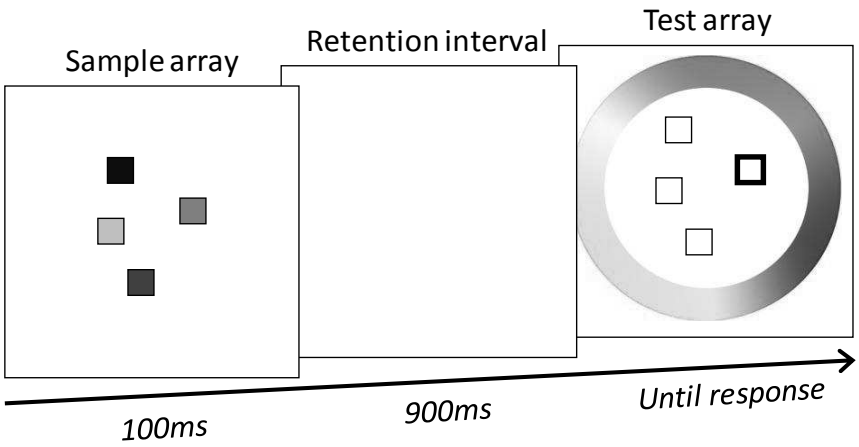


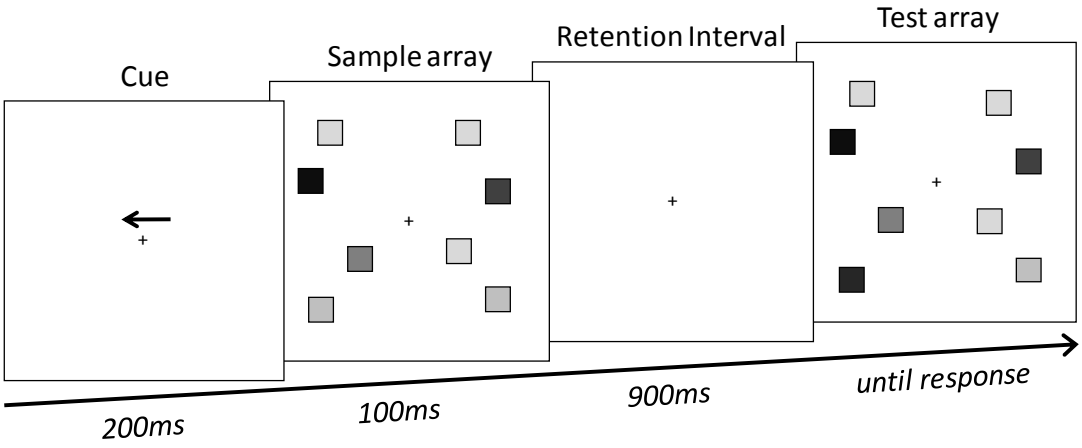
Figure 2. Example of a trial in a report procedure. The task is to retrieve the colour of the cued item and to indicate it on the colour wheel. Different grey levels represent different colours.

2.2. Neural measures

In recent years, Event Related Potentials (ERPs), which measure the electrophysiological activity in the brain, and Functional Magnetic Resonance Imaging (fMRI), which measures the change in blood flow that accompanies neural activity in the brain, have both contributed substantially to our understanding of brain organisation, including VSTM capacity. Contrary to the behavioural memory tasks in which the response is used to make assumptions about what is stored, these techniques can be used to track the on-line maintenance of information dynamically. One conclusion from recent ERPs (Vogel & Machizawa, 2004) and fMRI (Todd & Marois, 2004, 2005; Xu & Chun, 2006) studies is that the capacity limit of VSTM storage is localised to the occipital and posterior parietal cortex, even though VSTM is mediated by a large distributed network of brain regions (e.g., Cohen, Perlstein, Braver, Nystrom, Noll, Jonides, & Smith, 1997; Courtney, Ungerleider, Keil, & Haxby, 1997; Desimone, 1996; Fuster & Jervey, 1982; Miller, Erickson, & Desimone, 1996; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002).

ERPs studies used the Contralateral Control Method (Gratton, 1998), which is based on the fact that the visual system is primarily contralaterally organised. For example, Vogel and Machizawa (2004) presented participants with a bilateral display of equal amount of coloured objects in each hemifield. Participants were asked to fix centrally and to remember the items from a single hemifield for one second (Figure 3A). A large, sustained negative deflection, starting approximately 250-300 ms following the onset of the memory array and lasting during the entire retention period, was observed at posterior electrode sites that were contralateral to the attended hemifield. Importantly, the amplitude of this *contralateral delay activity* (CDA) (or *sustained posterior contralateral negativity* - SPCN) was found to be modulated by the number of memory items. Specifically, CDA amplitude was

the smallest when there was only one item in the memory array and increased as the number of items increased, reaching an asymptote limit at each individual's behaviourally measured capacity, typically at around 3-4 items (Figure 3B). These findings have since been replicated numerous times rather consistently (e.g., Anderson, Vogel, & Awh, 2011; Delvenne, Kaddour, & Castronovo, 2011; Gao, Xu, Chen, Yin, Shen, & Shui, 2011; Eimer & Kiss, 2009; Ikkai, McCollough, & Vogel, 2010; McCollough, Machizawa, & Vogel, 2007; see the review by Perez & Vogel, *in press*). The strong correlation between the amplitude of CDA and the number of objects held in memory suggests that this component is a good electrophysiological marker of VSTM capacity.



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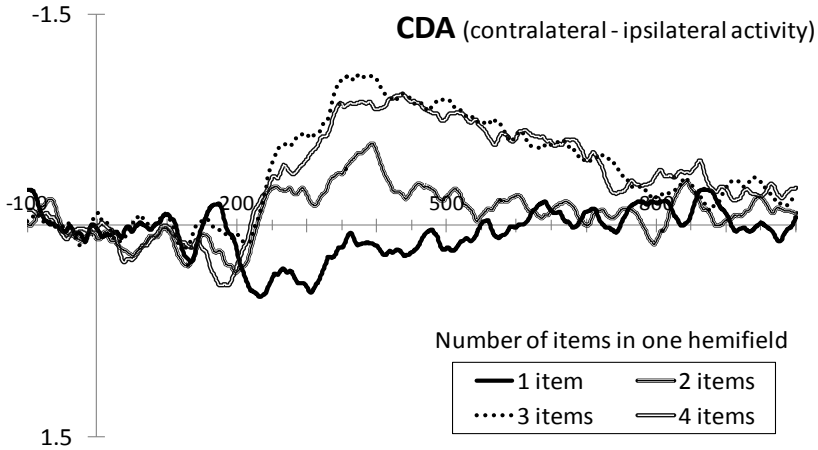


(B)

Figure 3. (A) Example of a trial used in ERPs studies. The different grey levels represent different colours. The task is to memorise the colours in the cued hemifield (indicated by the arrow). (B) CDAs (ipsilateral activity subtracted from contralateral activity) at posterior electrode sites for arrays of one, two, three, and four items per hemifield. (Adapted from Delvenne et al., 2011b.).

Neuroimaging studies using fMRI have also contributed to the study of VSTM capacity by revealing the involvement of specific brain regions, which are also sensitive to the number of items held in memory. In particular, reminiscent of CDA amplitude, the activity in the intraparietal sulcus (IPS) has been found to be strongly modulated by the number of objects that are held in memory and

to also reach an asymptotic limit at around 4 items (Todd & Marois, 2004; 2005; Xu & Chun, 2006). Furthermore, distinct cortical regions, including regions within the IPS, have been found to reflect distinct aspects of VSTM capacity (Xu, 2007, 2009; Xu & Chun, 2006, 2007). Whereas the activity in the inferior IPS has been found to be modulated by the number of locations occupied by the objects in the memory array, those in the superior IPS and the lateral occipital complex (LOC) are sensitive to the complexity of the objects. Note that the functional similarities between the IPS and the CDA, as well as the dorsal, posterior scalp topography of the CDA, strongly suggest that the IPS may be the major source of this wave. Furthermore, the dissociation between the two IPS regions could possibly resolve the current disagreement over whether CDA is primarily sensitive to the number of remembered objects or to the information load (Gao et al., 2011; Gao, Li, Liang, Chen, Yin, & Shen, 2009; Ikkai et al., 2010; Wang, Most, & Hoffman, 2009; Woodman & Vogel, 2008). Since such a large and sustained ERP component is likely to be generated by several coordinated sources of which both IPS regions may play a central role, it is plausible that the CDA amplitude is sensitive to both the number and the complexity of the objects held in memory. This remains an open question and further ERPs studies are needed to identify the temporal dynamics and the interactions between these two aspects of VSTM storage.

It is clear that the last 15 years of research into VSTM has come to a consensus according to which VSTM is extremely limited in storage capacity. The limited resources available to maintain visual information in short-term memory is shared between the representations of the items. As I will discuss this in the next section, it appears that both the number and resolution of representations are limited in VSTM (Wilken & Ma, 2004; Alvarez & Cavanagh, 2004; Awh et al., 2007; Scolari, Vogel, & Awh, 2008; Zhang & Luck, 2008) and correspond to separate dimensions of memory ability (Awh et al., 2007; Xu & Chun, 2006).

3. FACTORS INFLUENCING THE CAPACITY OF VISUAL SHORT-TERM MEMORY

3.1. Verbal recoding

Intuitively, we may assume that more visual objects can be retained in VSTM if those objects can be named and rehearsed phonologically. However, conflicting evidence exists as to whether the verbal recoding of visual information affects the number of items that can be held in VSTM at all. On the one hand, several studies have shown an increase in VSTM capacity when verbal memory is available to help with retention (Paivio, 1990; Postle, D'Esposito & Corkin, 2005; Silverberg & Buchanan, 2005). On the other hand, other studies have found that VSTM performance is unaffected by the occurrence of a concurrent task that occupies verbal memory (Phillips & Christie, 1977; Pashler, 1988; Vogel et al., 2001; Morey & Cowan, 2004; 2005; Eng, Chen & Jiang, 2005), suggesting that the prevention of verbal encoding does not reduce VSTM capacity. This recurrent failure to find a benefit of verbal recoding of information on VSTM capacity may be attributed either to the similarity between the capacity of verbal and visual short-term memory (Cowan, 2001), and/or to the cost that would be required by such an additional cognitive process of translating a visual object into a verbal code. Nevertheless, because of the current uncertainty of the role of verbal memory in VSTM capacity, the recommendation would be to use procedures that simply prevent verbal recoding of the to-be-remembered visual items. The three most common procedures that have been

used in the literature to minimize the role of verbal memory are (1) the use of a brief presentation of the memory items, which would reduce the ability to verbally encode the stimuli (Frick, 1988), (2) the use of meaningless and unfamiliar objects, that are difficult to be named, such as irregular shapes, textures, etc. (e.g., Cermack, 1971; Delvenne & Bruyer, 2004), and (3) the use of a concurrent verbal task (e.g., Delvenne & Bruyer, 2004; Delvenne et al., 2010; Vogel et al., 2001; Wheeler & Treisman, 2002; Xu & Nakayama, 2007).

3.2. Individual differences

While the storage capacity of VSTM in healthy adults might averaged around 3-4 items (Cowan, 2001; Luck & Vogel, 1997), there exist considerable differences across individuals, ranging from 1.5 items to about 5 items (Vogel & Machizawa, 2004; Vogel et al., 2001). It has been recently suggested that individual differences in VSTM capacity might reflect their ability to exclude irrelevant information from entering VSTM (Jost, Bryck, Vogel, & Mayr, 2011; Lee, Cowan, Vogel, Rolan, Valle-Inclan et al., 2010; McNab & Klingberg, 2008; Vogel, McCollough & Machizawa, 2005). For instance, using the Contralateral Control Method (Gratton, 1998),Vogel and colleagues (2005) recorded the electrophysiological activity in participants while they performed a change detection task in which two or four oriented bars were displayed in the cued hemifield. In some trials, all the items were red (i.e., two- and four-targets conditions) whereas in other trials two were red and two were blue (i.e., distracters-present condition).The task was to remember only the red items. Participants were split into two groups based on their K scores (Cowan, 2001; Pashler, 1988): a high and a low capacity group. In high capacity individuals, the CDA amplitude was significantly smaller in the distracters-present condition than in the four-targets condition, but was equivalent to that observed in the two-targets condition, indicating that these individuals were efficient at filtering out the distracters and at preventing them from consuming memory capacity. By contrast, the CDA amplitude in low capacity individuals was larger in the distracters-present condition than that in the two-targets condition, but did not differ from that in the four-targets condition, indicating a high level of inefficiently from these individuals at excluding irrelevant information from entering memory. Furthermore, using the fMRI, McNab and Klingberg (2008) found that the activity in the prefrontal cortex and basal ganglia was a reliable predictor of (1) the extent to which irrelevant information is excluded from being stored in memory, and (2) individual differences in memory capacity. Moreover, the deficit for low-capacity individuals in filtering out irrelevant information appears to be restricted to spatial-based filtering mechanisms and reflects a difficulty in disengaging attention from the location of the distracters (Jost et al., 2011; Fukuda & Vogel, 2009, 2011). When irrelevant items share the same spatial location as relevant items, no differences between low- and high-capacity individuals in the ability to prevent distracters from entering VSTM is observed, suggesting a distinction between the mechanism for the feature-based filtering and that for spatial-based filtering (Zhou, Yin, Chen, Ding, Gao, & Shen, 2011). Specifically, Zhou and colleagues (2011) found that once relevant information enters VTSM, irrelevant high-discriminable information that shares its spatial location is also transferred into VSTM, regardless of VSTM capacity. As we will see in Section 3.5., one possible explanation for the absence of a deficit in feature-based filtering in low-capacity individuals may be that once features share the same spatial location, they are automatically bound into an integrated representation at no cost.

3.3. Age

Research in developmental studies has found that the capacity of VSTM increases throughout childhood. For example, it has been shown that infants of a few hours old have a capacity of only one object (Slater, Earle, Morison, & Rose, 1985; Slater & Morison, 1991). While it is acknowledged that the ability to remember one visually presented object is present very early in development, the age at which VSTM maturity is attained is a matter of debate. Some authors have suggested VSTM capacity increases during the first year of life to the adult levels of approximately 4 objects (Rose, Feldman, & Jankowski, 2001; Ross-Sheehy, Oakes, & Luck, 2003). Others have proposed that children might wait until the age of about 5 before they can double in size their capacity of one object (Cowan, Elliott, Saults, Morey, Mattox, et al., 2005; Riggs, McTaggart, Simpson, & Freeman, 2006) and that the full VSTM maturity is only reached at 10-11 years of age (Cowan et al., 2005; Logie & Pearson, 1997; Riggs et al., 2006; Wilson, Scott, & Power, 1987). The distinction between object individuation and identification (Xu, 2007, 2009; Xu & Chun, 2006, 2007, 2009) may provide a possible framework to explain those conflicting findings. Research has shown that whereas infants of 10 months old are able to keep track of more than one object when presented simultaneously at different locations, they can only infer the presence of one object when the objects are presented sequentially at the same location (Xu & Carey, 1996). This suggests that inferring the number of objects present depends greatly on whether the objects occupy distinct spatial locations. Infants may therefore use spatial information to individuate multiple objects very early in development (by using the output from the inferior IPS, responsible for object individuation), but may only process more than one object in more details (object identification) later. Therefore, it is possible that a capacity of 3-4 objects can be found in children at the end of their first year if the task does not entail processing the objects in much detail. Clearly further research is needed to examine this assumption. Note that at the other extreme of the age range, VSTM capacity declines in elderly people (e.g., Hartley, Little, Speer, & Jonides, 2011; Jost et al., 2010). While lifespan changes in VSTM capacity are well documented, the underlying neuronal and functional mechanisms still need to be understood.

3.4. The nature of the memory representations

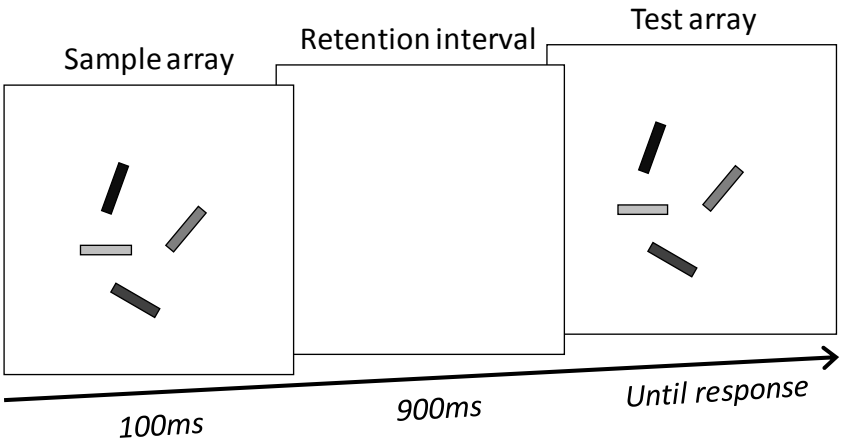
The capacity of VSTM has been shown to be influenced by the nature of the memory representations. For example, VSTM capacity is larger when the to-be-remembered visual items belong to distinct dimensions, such as colour, shape, orientation, texture, etc., as compared to when they all belong to the same single dimension (e.g., colour) (Delvenne & Bruyer, 2004; Wheeler & Treisman, 2002). For instance, using the change detection paradigm (Phillips, 1974), we found that remembering two shapes and two textures (thus four features in total) was easier than remembering four shapes or four textures, suggesting that items from the same dimension compete for capacity, whereas items from different dimensions may be maintained in independent memory stores (Delvenne & Bruyer, 2004). The existence of distinct memory stores for each specific dimension is supported by recent neuroimaging studies that suggest that the neural mechanisms that encode the sensory information are the same as those that store it (Awh & Jonides, 2001; Chelazzi, Miller, Duncan, & Desimone, 1993; Harrison & Tong, 2009; Miller, Erickson, & Desimone, 1996; Postle, 2006; Serences, Ester, Vogel, & Awh, 2009; Supèr, Spekreijse, & Lamme, 2001). For example, Serences and colleagues (2009) used the fMRI and found specific patterns of sustained neural activities for each remembered dimension (i.e., the colour or orientation of a foveally presented grating) in primary visual cortex (V1) during VSTM maintenance. Those patterns were similar to those observed during the encoding of the same stimuli.

In addition, other recent studies have suggested that the complexity of the objects may also influence the number of objects that can be held in memory. VSTM capacity has been shown to decrease as object complexity increases (Alvarez & Cavanagh, 2004; Awh et al., 2007; Eng et al., 2005; Luria & Vogel, 2011; Scolari et al., 2008; Xu & Chun, 2006). For instance, Alvarez and Cavanagh (2004) observed that the capacity of VSTM was approximately four objects when the stimuli were simple coloured squares, but it was reduced to only two objects when the stimuli were random polygons. At the neural level, object complexity may be represented in the superior IPS and the LOC. Xu and Chun (2006) found that the activity in those areas increased with both the number and the complexity of objects held in memory. However, while this activity reached an asymptotic limit at approximately four objects when simple objects were used (i.e., solid shapes), it did not increase above two objects when complex objects were used (i.e., various shaped holes) (see also Song & Jiang, 2006).

The emotionality of the objects has also been suggested to affect VSTM capacity. For example, recent studies have found that VSTM capacity was enhanced for emotional faces, such as angry (and sometimes happy) faces, as compared to neutral faces (Jackson, Wolf, Johnston, Raymond, & Linden, 2008; Jackson, Wu, Linden, and Raymond, 2009; Langeslag, Morgan, Jackson, Linden, & Van Strien, 2009). The perceptual and cognitive mechanisms underlying the VSTM advantage for a particular emotional object are currently unknown. In the case of an angry face, its perception may represent a potential threat situation. Thus, the aptitude to effectively encode and hold in memory the face of an angry individual has perhaps developed particularly well in order to deal effectively with such a potential menace.

3.5. The perceptual organisation of visual information

One of the factors that probably influence the most VSTM capacity is the perceptual organisation of visual information in the visual field. In particular, the integration of several to-be-remembered visual features into a single object can considerably increase the number of features that can be held simultaneously in memory. For example, a shape and a colour will be better remembered if they belong to the same object (i.e., a coloured shape) than if they form two distinct entities. The first compelling demonstration of the effect of feature integration on VSTM capacity was provided by Luck and Vogel (1997). In their landmark study, Luck and Vogel demonstrated that individuals were able to store up to four colours or orientations at a time, but when the colours and orientations were conjoined to form four coloured orientations, they were able to retain all eight features (see Figure 4). The authors replicated these findings with objects containing each four features (colour, size, orientation, and the presence or absence of a gap in the centre of the object). They found that all features (i.e., 16 features) from four objects can be remembered as accurately as four features distributed across four objects. This clearly shows that the integration of features into objects increases substantially the number of features that can be stored in VSTM. Although Luck and Vogel (1997)'s study provides evidence that in some cases VSTM capacity may be defined by the number of integrated objects, studies on object complexity have shown that the formation and encoding of a complex object requires more resources than a simple object and that VSTM capacity decreases as function of object complexity (Alvarez & Cavanagh, 2004; Awh et al., 2007; Eng et al., 2005; Luria & Vogel, 2011; Scolari et al., 2008; Xu & Chun, 2006). This suggests that VSTM capacity may not be only determined by the number of objects, but also by the information load.



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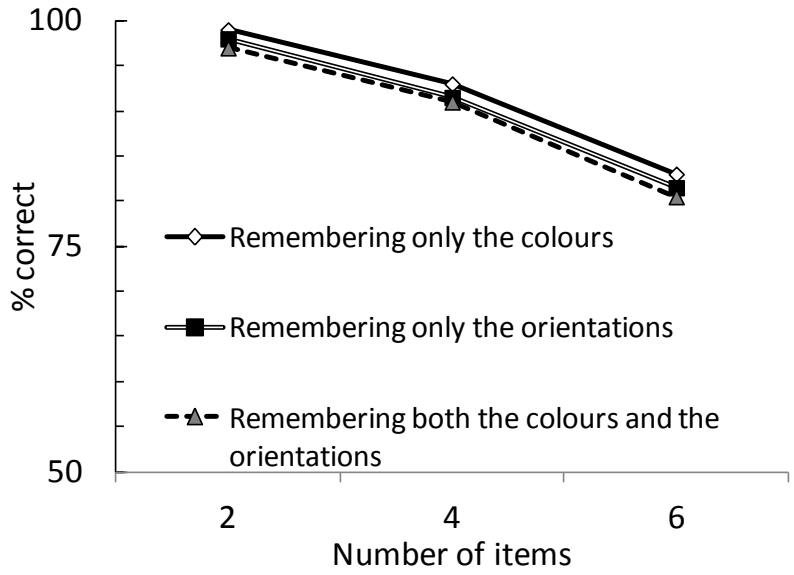

(B)

Figure 4. (A) Example of a trial adapted from Luck and Vogel (1997). The different grey levels represent different colours. The task is to memorise the colours, the orientations, or both. (B) Results adapted from Luck and Vogel (1997) and showing similar memory performance across the three conditions.

The effect of perceptual integration on VSTM capacity greatly depends on the nature and spatial arrangement of features within objects. Features can be bound together in VSTM and stored just as well as a single feature, provided that the features belong to different dimensions (i.e., colour, shape, orientation, etc.). When the features are from the same dimension, the integration of those features into a smaller number of objects has no effect on VSTM capacity (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Wheeler & Treisman, 2002; Xu, 2002a). For example, four unicoloured objects are stored in memory just as well as two bicoloured objects, suggesting that features from the same dimension compete for memory capacity. In addition, in the real world, most visual objects are composed of multiple parts, each with its own features. For example, a car consists of a combination of different parts (i.e., doors, wheels, windows, etc.), which have each their own shape, size, colour, etc. Studies have shown that memory improves when the features are integrated into the same part of an object, thus sharing the same spatial location, compared to different parts of an object (Delvenne & Bruyer,

2004; Xu, 2002b). For example, if a shape feature appears on one part of an object and a texture feature on another part of the object, then individuals perform worse when required to remember those features than when the shape and the orientation feature appear on the same part of an object (Delvenne & Bruyer, 2004).

Most of the time in the real world, we are confronted to multiple objects that appear at distinct spatial locations within our visual field. The spatial configuration of a visual display, defined by the spatial relationships between objects, seems to be automatically encoded in VSTM, even prior to the objects themselves (Chun & Jiang, 1998; Jiang et al., 2000). For example, performance at a colour change detection task is reduced if the spatial configuration changes between the memory and test array (Jiang et al., 2000), indicating that an object from a multiple objects display is not independently stored in memory but rather in relation to the others. Moreover, the spatial configuration of a visual scene is not only encoded in VSTM, but it may even help retaining the objects themselves. Memory capacity for objects is reduced if the formation of a spatial configuration is either prevented or useless for detecting a change between a memory and test array (Delvenne et al., 2002; Delvenne & Bruyer, 2006).

3.6. Perceptual expertise

Developmental and aging studies have indicated that once VSTM capacity reaches its maturity in childhood (at about 3-4 items), it remains stable all through adulthood and declines at the end of life. This indirectly suggests that VSTM capacity may be rather inflexible and that the adult human brain does not exhibit plasticity for capacity. However, recent work suggests that extensive experiences with a specific object category can result in superior object identification performance and increase VSTM capacity (see Curby & Gauthier, 2010). For example, VSTM capacity for faces, stimuli for which we are expert, is larger than that for other complex non-face objects, such as clocks and cars (Curby & Gauthier, 2007). Moreover, more upright faces can be remembered than inverted faces (Curby & Gauthier, 2007; Scolari et al., 2008) and more famous faces can be stored in memory than unfamiliar faces provided that the faces are presented upright, that is to say in an orientation that is familiar to us (Jackson & Raymond, 2008). The effect of perceptual expertise on VSTM capacity does not appear to be tied to the face category. Car experts, but not car novices, also demonstrate a VTSM advantage for upright, but not inverted, cars similar to that for faces (Curby, Glazek, & Gauthier, 2009). Importantly, VSTM capacity for upright cars appears to be correlated with each individual's degree of car expertise. The underlying mechanisms responsible for the advantage of perceptual expertise for VSTM capacity remains to be understood. However, one plausible explanation may be that extensive experiences with a particular object category reduce the perceived complexity of the objects, perhaps by a more holistic encoding process that facilitates the integration of features within objects of expertise (Curby & Gauthier, 2010). To further examine the role of perceptual expertise in reducing the perceived perceptual complexity of the objects, it would be interesting in future studies to examine the correspondence between the level of expertise for a particular object category and the neural activity in the superior IPS and LOC, namely the areas that have been shown to be sensitive to the complexity of objects in VSTM (Xu & Chun, 2006).

3.7. The spatial distribution across the left and right hemifields

Recent data have suggested that the capacity of VSTM can benefit from the division of visual inputs across the two hemifields. For example, using a change detection task, I found that the spatial locations of items were better remembered when the items were split between the left and right side of fixation than when they were all presented within the same single hemifield (Delvenne, 2005). This bilateral benefit in visual information processing is known as the *Bilateral Field Advantage* (BFA) and refers to the fact that visual tasks are processed more accurately and/or more quickly when the visual information is distributed across the vertical meridian than when it is displayed in one hemifield only. Over the last 40 years, studies have revealed this phenomenon in a number of distinctive visual tasks, such as target identification tasks (Awh & Pashler, 2000; Chakravarthi & Cavanagh, 2006; Dimond & Beaumont, 1971; Scalf, Banich, Kramer, Narechania, & Simon, 2007), target detection tasks (Alvarez & Cavanagh, 2006; Castiello & Umilta, 1992; Reardon, Kelly, & Matthews, 2009), visual enumeration tasks (Delvenne, Castronovo, Demeyere, & Humphreys, 2011), multiple object tracking tasks (Alvarez & Cavanagh, 2005), and matching tasks (Dimond and Beaumont, 1972; Banich & Belger, 1990; Belger & Banich, 1992, 1998; Berger, 1988; Brown, Jeeves, Dietrich, & Burnison, 1999; Collin, McMullen, & Seguin, 2009; Compton, 2002; Davis & Schmit, 1971; Koivisto, 2000; Kraft, Muller, Hagendorf, Schira, Dick, Fendrich, & Brandt, 2005; Kraft, Pape, Hagendorf, Schmidt, Naito, & Brandt, 2007; Liederman, Merola, & Martinez, 1985; Ludwig, Jeeves, Norman, & DeWitt, 1993; Muller, Malinowski, Gruber, & Hillyard, 2003; Norman, Jeeves, Milne, & Ludwig, 1992; Reuter-Lorenz, Stanczak, & Miller, 1999; Sereno & Kosslyn, 1991; Weissman & Banich, 2000; Weissman, Banich, & Puente, 2000; Zhang & Feng, 1999).

If a BFA is observed in visual processing, it is plausible to suggest that a BFA may also be seen in memory, especially considering the close relationship between perception and memory. For instance, it has been shown that the brain regions that are activated during sensory information encoding are also recruited during the maintenance of the information in VSTM (Awh & Jonides, 2001; Chelazzi et al., 1993; Harrison & Tong, 2009; Postle, 2006; Miller et al., 1996; Serences et al., 2009; Supèr et al., 2001). However, although a BFA in visual processing has been rather consistently found, research in VSTM has shown that the occurrence of this effect in memory seems to depend greatly on the nature of the visual information and the task. Specifically, a BFA has been observed in VSTM when the task is dominated by spatial processing, such as remembering multiple spatial locations (Delvenne, 2005) or spatial orientations (Umemoto et al., 2010), detecting the location of a change in a change detection task in which a change appears in all trials (Buschman, Siegel, Roy, & Miller, 2011), and attending to two locations within memory representations (Delvenne & Holt, in press). By contrast, when spatial processing is minimized in the task, the distribution of visual inputs across the two hemifields does not increase VSTM capacity. In particular, no BFA has been found in VSTM when the task entails detecting a non-spatial attribute (i.e., colour) change between two successive displays (Delvenne, 2005; Delvenne et al., 2011b; Mance, Becker, & Liu, 2011; Umemoto et al., 2011; Xu & Nakayama, 2007) or when the task involves reporting letters (Duncan et al, 1999). Clearly, further research is needed to fully understand the BFA in VSTM, to determine its source, and to identify the perceptual and cognitive factors that affect its occurrence.

4. CONCLUSION

The last 15 years has seen surge in both cognitive neuroscience and behavioural research on VSTM. Much of this research has been devoted to characterize its capacity limit and to understand the factors that modulate it. At present, there is general agreement that VSTM is extremely limited in the number of items it can store. Although the limitation is estimated to be around 3-4 items, research has also shown that the capacity is affected by a number of factors, which certainly complicates any attempt to provide a pure estimate of VSTM capacity. Specifically, putting on one side the effects of distraction, fatigue, or other external factors that could affect the general performance on a memory task, the number of visual items that you can hold in memory depends on your age, your previous experience with the items, the nature and complexity of the items and how they are perceptually organised within your visual field.

The fact that VSTM capacity is not fixed but can be modulated by different factors strongly suggests that VSTM is limited by some resources that are flexibly allocated. Research on object complexity, in particular, has provided clear evidence that VSTM capacity decreases as function of object complexity (Alvarez & Cavanagh, 2004; Awh et al., 2007; Eng et al., 2005; Luria & Vogel, 2011; Scolari et al., 2008; Xu & Chun, 2006), indicating that the more each item requires resources, the less items can be processed and held in memory simultaneously. How exactly those limited resources are allocated, however, is a question that remains yet to be resolved. Currently, two contrasting views have been proposed. For some researchers, resource allocation is discrete and quantised into 'slots' (Luck & Vogel, 1997; Zhang & Luck, 2008). According to this view, increasing the complexity of the objects may reduce the number of objects (or 'slots') that can be held in memory, but not the resolution of the remembered items. This slot model is an all-or-nothing model, where items are either stored in memory with high-resolution or not retained at all. For other researchers, resource allocation is continuous and divided among the items, with the resolution of the stored items reduced as their number increases (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Huang, 2010; Wilken & Ma, 2004). Rather than being an all-or-nothing model, this resource model proposes that items can be stored in VSTM with a low resolution.

The recent neural object-file theory, proposed by Xu and Chun (2006, 2007, 2009), may reconcile those two views, as it suggests that VSTM is limited by both a fix number of slots and the complexity of the representations. Specifically, this theory proposes that the inferior IPS selects a fix number of approximately four items via their spatial locations (object individuation) and that the superior IPS and the LOC process a subset of those items in more detail (object identification). If the items are simple and/or do not require much resources, then the capacity of VSTM will be limited by the object individuation stage. By contrast, if the items are complex and/or do require much resources, then only a subset of the selected items will be processed by the object identification stage and VSTM capacity will be reduced accordingly. Thus, the number and resolution of items held in VSTM may represent two distinct attributes of the VSTM representations and they may both define its limitation. Note that given that each hemifield may have some degree of resources independence in visual processing (Alvarez & Cavanagh, 2005; Delvenne, 2005; Buschman et al., 2011), it would be exciting in future studies to examine the correspondence between such hemifield independence and the dichotomy between number and resolution. One possibility, although rather speculative at this stage, has been nicely formulated by Buschman and colleagues (2011): "the two hemifields act like discrete resources, whereas within a hemifield neural information is divided among objects in a graded fashion" (p3).

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